SHORTER CONTRIBUTIONS

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Reproductive Ecology and Growth of a Captive Population of Little Colorado Spinedace (*Lepidomeda vittata*: Cyprinidae)

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The Little Colorado spinedace (*Lepidomeda vittata*; Tribe: Plagopterini) is a small ($\leq$ 138 mm total length) native cyprinid currently restricted to north-flowing tributaries of the Little Colorado River in Apache, Coconino, and Navajo Counties, Arizona. The species was originally described from specimens collected from the Little Colorado River near its headwaters in the White Mountains of eastern Arizona (Wheeler, 1889). Although there were only four collection records of *L. vittata* prior to 1939, Miller (1961) suggested that this cyprinid was once abundant in the Little Colorado River and its north-flowing tributaries, and perhaps in the Zuni watershed south of Gallup, New Mexico.

Extensive surveys throughout the known range of *L. vittata* during 1960 found only one specimen of this cyprinid in Clear Creek, Arizona (Miller, 1961); however, a large population was found in East Clear Creek, during 1961 (Miller, 1963). Surveys conducted by Minckley and Carufel (1967) in 1963 and 1966 found *L. vittata* throughout its known range in Arizona; however, populations declined again after this period (Minckley, 1973). Due to a sporadic distribution and a reduction in numbers, *L. vittata* was listed as threatened by USFWS in 1987 (U.S. Fish and Wildlife Service, 1987. Recently, Blinn et al. (1993) and Rinne and Alexander (1995) demonstrated, by in situ cage experiments, that predation by *Oncorhynchus mykiss* (rainbow trout) may, in part, be responsible for the disjunct and sporadic geographic distribution of *L. vittata*.

The limited information on *L. vittata* suggested that additional studies were needed to enhance our understanding of the general habitat requirements and reproductive ecology of this threatened native cyprinid. This study describes the life history of a transplanted, captive population of *L. vittata* in an earthen pond near Flagstaff, Arizona, during 1994 and 1995. Our study focused on spawning, growth, and the general ecology of *L. vittata*.

MATERIALS AND METHODS

The Aboretum stream/pond is an earthen pond located in Sinclair Wash, 6.5 km south-southwest of Flagstaff, Arizona (elevation 2167 m; 35°9′N, 111°43′W). The pond is oval in shape (38 m $\times$ 47 m, 125 m perimeter) with a surface area of 1408 m^2 and a maximum depth of 3.6 m. The stream (35 m long, 1–2 m wide, $\leq$ 0.25 m deep) is formed from recirculated water pumped underground from the pond into the stream which drains by gravitational flow back into the pond. On 2 September 1992, 44 *L. vittata* were collected from Rudd Creek in eastern Arizona (elevation approxmiately 2100 m) and introduced into the stream/pond. Total lengths (TL) of fish ranged from 58 to 120 mm ($\bar{x}$ = 85.9 mm; SE $\pm$ 1.7, n = 44). The transplants were estimated to be about one year old based on subsequent growth measurements taken in the pond. There were no fish in the habitat prior to the introduction of *L. vittata*; however, tiger salamanders (*Ambystoma tigrinum*) were present.

Water temperature and dissolved oxygen were measured at 20-cm intervals throughout the water column with a YSI model 55 m at approximately biweekly intervals between April and September 1994, bimonthly intervals between September 1994 and March 1995, biweekly intervals from April to August 1995, and monthly intervals from September to November 1995. Water temperatures were taken periodically under the ice each year. Water transparency (Secchi depth) was taken concurrent with measurements of temperature and dissolved oxygen. All measurements were taken between 1030 and 1400 h. Light energy was measured with a Li-Cor Quantum Photometer (Model LI-185B) throughout the day during spawning events. Daily maximum and minimum air temperatures were recorded by Arboretum personnel during 1994 and 1995.

Four gravel trays (0.5 $\times$ 0.5 m) were placed along the pond shoreline ($\leq$ 0.3 m in depth) during May and June of 1994 and the pond shoreline and stream (n = 4 per habitat) during the same months of 1995 to evaluate the importance of gravel substrata in spawning. Observations were made on and around the trays which were removed periodically and examined for eggs. Observations on spawning were also made in the stream/pond every 2–3 days during May and June of 1994 and 1995.

The dimensions of 100 stones were measured from random collections at five sites in the stream where spawning occurred. Current velocity was measured at each site (n = 5) with a Marsh-McBirney electronic flow meter (Model 201) along with water depth (n = 5).

The entire shoreline (0–4 m from shore) of the pond was seined (1.4 m × 5 m; 3.5 mm mesh size) at weekly intervals from June through September and on 11 November during 1994. Seine collections were taken at triweekly intervals between April and September during 1995 and on 4 October and 3 November 1995. Fry and larvae (≤ 20 mm) were collected with aquarium nets (17 × 25 mm; 1 mm mesh size) during and after spawning to monitor the modal size of each cohort. Standard and total lengths and live wet weights were taken for each fish, and sex and reproductive condition were taken for adults. Wet weights (weighed within 30 sec after removal from water) were measured to the nearest 0.0l g on a top loading balance (Ohaus, Model CT 200-S) in the field. Larvae were weighed to the nearest 0.001 g on an analytical balance (Mettler, Model H20T) in the laboratory. Males and females were considered ripe when gametes were expressed with moderate pressure to the abdomen (Synder, 1992). Standard length to weight regression equations were calculated for fish ≥ 35 mm. Values were log-log transformed, and the significant difference between regression equations for each sex was tested by analysis of covariance (Zar 1984).

Vertical net tows (0.5 m net diameter, 250 μm mesh) were taken in the pelagic (3 m, n = 10) and littoral (≤ 0.5 m, n = 10) zones on 1 June 1994 to determine the distribution of larvae and fry (≤ 20 mm) *L. vittata* in the pond.

RESULTS

No ripe *L. vittata* were observed in collections taken during early April 1994 when temperatures throughout the water column were ≤ 13 C (Table 1). However, on 26 April over 58% of the males (n = 54) were ripe, but no females were gravid (n = 28). Temperature in the top meter at this time averaged ≥ 16.0 C (SE ± 0.8), whereas the bottom 2 m averaged 8.2 C (SE ± 1.2), and water transparency was low (Secchi depth ≤ 70 cm). The bottom l m of the pond was anoxic and remained in that condition until late-September, whereas the top 2 m averaged 8.5 mg/L (± SE 0.4) dissolved oxygen. By 7 May, temperatures in the surface meter remained at 16.0 C and rose to 13.8 C (SE ± 0.6) in the lower section of the pond. At this time, 75% of the males (n = 48) and 98% of the females (n = 22) were ripe (Table 1). Males were ripe at ~ 70 mm in TL, whereas females were normally not ripe until 80 mm TL. The highest frequency of ripe females occurred during May when temperature ranged from 16 to 18 C and water transparency was ≤ 100 cm (Table 1). The reduced water transparency was caused by snow melt inflow from Sinclair Wash. No ripe fish were captured after early August even though water temperatures were ≥ 16 C throughout the remainder of August and September.

During 1995, no ripe *L. vittata* were taken until late April (Table 1). Water temperatures fluctuated greatly during April and May and were 3–6 C lower than those of the previous year. The variation in population frequency of sexually mature males also fluctuated during May, and no ripe females were collected until 26 May. The cool conditions resulted in a 2–3 week delay in the development of ripe females during 1995 and reduced the size of age-0 fish by as much as 14 mm TL; fish overwintered at < 40 mm TL. The frequency of ripe *L. vittata* declined throughout the summer with no ripe males or females collected after early July (Table 1).

Spawning was first observed in the stream between 16 and 20 May during 1994, whereas spawning was delayed by at least two weeks in 1995 (Fig. 1). Spawning runs into the stream typically occurred between 1030 and 1530 h, and frequently coincided with the period when the stream mouth was in direct sunlight. Fish were rarely observed in the stream prior to and after this period, and no spawning was observed at night with indirect light from flashlights. Light energy at the water surface near the stream mouth ranged from 2000 to 2400 μE m^{-2} s^{-1} during active spawning, and water temperature ranged from 19 C to 22 C.

At the onset of spawning, small schools (10–40) of adult fish separated from larger schools of up to 120 fish and ascended the stream. Typically, a group of 10–15 males hovered around one gravid female over gravel substrata, each periodically bumping and nibbling the vent region of the female. Over 95% of the males participating in the spawn were ripe, and at least 75% of the females were gravid. Spawning fish

TABLE 1. MEAN WATER TEMPERATURE (± SE) IN THE TOP 1 m OF THE WATER COLUMN, SECCHI DEPTH (cm), PERCENT RIPE ADULT MALES AND PERCENT GRAVID ADULT FEMALES IN THE ARBORETUM POND NEAR FLAGSTAFF, ARIZONA, FOR SELECTED DATES DURING 1994 AND 1995. * Reduction in light penetration due to cyanobacteria bloom. Number of fish examined for each sex on each date is in parentheses following percentages.

Date	$\bar{x}$ temperature (C) in top meter	Secchi depth (cm)	% ripe males (≥ 70 mm TL)	% gravid females (≥ 80 mm TL)
04/06/94	12.5 ± 0.9	48	0.0 (28)	0.0 (22)
04/14/94	15.8 ± 0.8	70	10.2 (32)	0.0 (31)
04/26/94	16.4 ± 1.4	70	58.3 (89)	0.0 (63)
05/07/94	16.0 ± 1.2	70	75.0 (69)	98.0 (57)
05/23/94	16.2 ± 1.0	90	82.4 (82)	91.0 (63)
06/01/94	18.3 ± 0.5	225	98.0 (53)	50.0 (48)
06/08/94	18.5 ± 0.2	230	97.2 (63)	18.2 (36)
06/14/94	19.1 ± 0.2	235	49.2 (39)	11.0 (33)
06/28/94	20.0 ± 0.2	235	34.7 (34)	9.1 (29)
07/27/94	19.6 ± 0.3	300	30.0 (78)	12.5 (71)
08/02/94	20.8 ± 0.3	300	7.1 (54)	7.7 (42)
08/25/94	22.7 ± 0.2	300	0.0 (59)	0.0 (50)
09/28/94	15.9 ± 0.2	300	0.0 (51)	0.0 (34)
11/11/94	6.1 ± 0.06	350	0.0 (18)	0.0 (12)
02/17/95	1.8 ± 0.03	ice cover	0.0 (31)	0.0 (26)
04/05/95	12.4 ± 1.1	90	0.0 (163)	0.0 (121)
04/28/95	7.7 ± 1.3	24	2.4 (99)	0.0 (58)
05/09/95	10.8 ± 1.2	39	4.7 (43)	0.0 (54)
05/19/95	13.3 ± 1.4	55	30.9 (127)	0.0 (98)
05/22/95	17.3 ± 1.3	55	8.7 (56)	0.0 (47)
05/26/95	13.6 ± 0.9	60	37.0 (72)	5.6 (63)
05/28/95	14.3 ± 0.9	65	43.9 (81)	15.7 (57)
06/05/95	17.5 ± 1.2	80	45.5 (72)	14.3 (59)
06/21/95	21.7 ± 1.0	115	32.3 (91)	0.0 (82)
07/03/95	19.8 ± 0.5	300	19.4 (45)	0.0 (48)
08/02/95	20.6 ± 1.1	60*	0.0 (44)	0.0 (38)
09/08/95	19.7 ± 0.4	65*	0.0 (43)	0.0 (45)
10/04/95	14.3 ± 0.3	121	0.0 (38)	0.0 (31)
10/30/95	10.2 ± 0.5	255	0.0 (86)	0.0 (57)

* Reduction in light penetration resulted from a dense cyanobacteria bloom of *Anabaena circinalis* Rabh. and/or *A. spiroides* v. *crassa* Lemm.

were highly tuberculate and exhibited brightly colored orange-red patches at the base of their paired fins with the patches more intense on males than on females.

Indentations were formed in the gravel and substrata were cleared of sediment by swarming adults at spawning sites. During spawning, males and females were side by side, on top of each other, twisting around each other, with rapid posterior movements, and occasional dorsal-ventral inversions that flashed the silvery side of the fish. In some instances, males were nose down in the substratum with caudal fins emerging from the stream during the spawning event. Bouts of spawning behavior typically lasted for 10–20 min for each pair.

Eggs stripped from females during spawning were in a sticky mass. In one large gravid female (97 mm in TL; 10.13 g), nearly 1 g of egg mass was artificially expressed. Mature eggs (1.0–1.3 mm in diameter) were yellow to orange-red in color, whereas immature eggs where white to pale yellow.

Spawning occurred over substrata with mean stone diameters of 6.4 mm (± 0.37), with smallest stones about 2 mm and largest stones up to 16 mm. No spawning was observed in stream pools with fine sediment, in coarse gravel (> 25 mm in diameter), in aquatic vegetation or over gravel trays placed around the shoreline of the pond. In contrast, heavy spawning activity occurred over gravel trays placed in the stream, with over 100 fertilized eggs retrieved from trays. Typically, ripe females spawned over substrata with mean current velocities of 14.2 cm s^{-1} (SE ± 0.3) and average water depths of 3.8 cm (SE ± 0.1). Based on the size structure of the population, we estimated three spawns occurred between May and mid-June during 1994 and 1995.

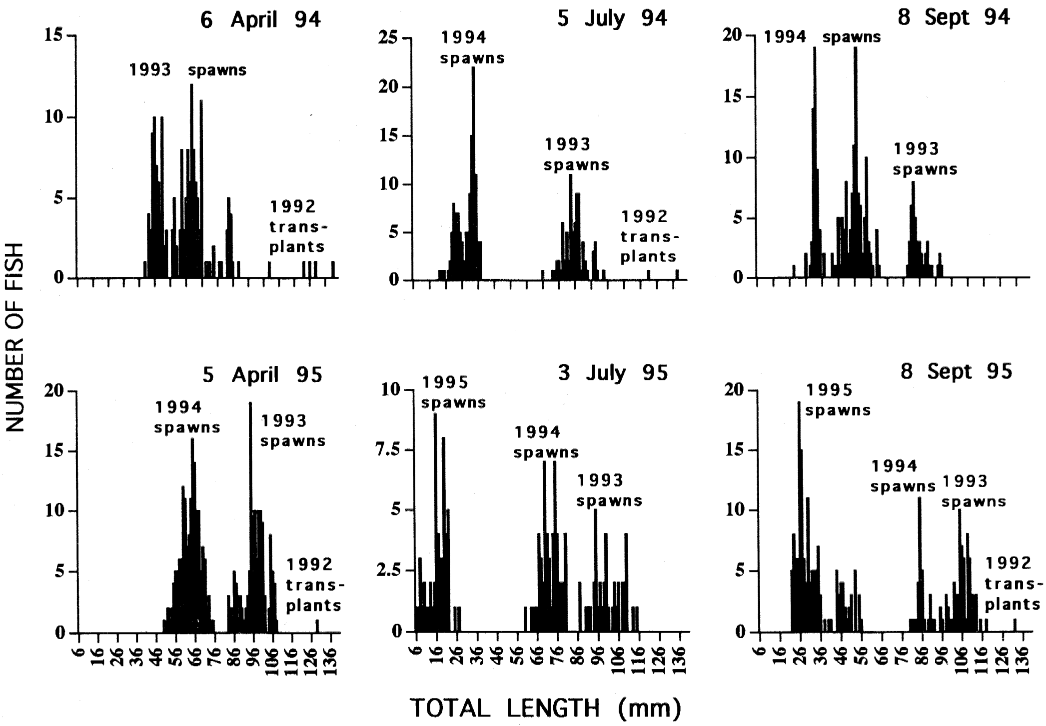

Fig. 1. Size frequency distribution of the captive Little Colorado spinedace (*Lepidomeda vittata*) population in the Arboretum pond at Flagstaff, Arizona, during 1994 and 1995.

Larvae were first observed in the stream and stream/pond interface within five days after spawning. Newly hatched larvae ranged from 6–7 mm in TL and weighed ≤ 0.004 g; fins were formed when fish were ≥ 11 mm TL. All larvae moved into the pond and remained along the shallow shoreline (≤ 2 cm in water depth) near aquatic vegetation, especially floating algal mats. Fish moved into deeper water once they attained ≥ 20 mm in TL. Larvae and/or juveniles (11–20 mm) did not remain in the stream.

Fish aggregated at their smallest larval stage and immature *L. vittata* (20–25 mm in TL) exhibited a schooling behavior which persisted into adulthood. At 20–25 mm TL, fish were observed swimming in schools of up to 60 fish near the shore in water depths of ≤ 40 cm. No fish < 25 mm in TL were collected in water > 0.75 m in depth. All fish moved away from the shoreline into deeper water (> 1.5 m) by early October when the anaerobic zone disappeared from the pond bottom.

The original *L. vittata* transplants (2 Sept. 1992) were typically ≥ 100 mm in TL by November 1993; the average TL of introduced fish was 85.9 mm (SE ± 1.7). The transplants were readily identified through 8 September 1995, however, were increasingly difficult to discern by early 1995 due to recruitment by 1993 cohorts (Fig. 1). Our tracking of the transplants over the two years of study suggested that *L. vittata* has a lifespan of at least four years of age.

Distinct cohorts of *L. vittata* were identified over the two-year period (Fig. 1). There was a linear increase in modal size for each cohort throughout the summer and early fall. The modal size of each cohort increased 3–4 mm in TL per week between late May and late August. Fish attained about 50% of their adult TL in two months. Growth rate was reduced to ≤ 2 mm in TL per month between mid-September and the end of November with little growth during ice cover. The relationship ($r^2 = 0.996$) between TL and SL is expressed by the equation: $SL = 0.809 \cdot TL + 0.992$. The modal fish weight in the first cohort during 1994 was 0.32 g after one month, 1.47 g after two months, and 2.2 g per fish after three months. A similar rate of growth occurred during 1995. Most fish ≥ 100 mm in TL were females (78%). The linear relationship between weight and SL for male and female fish was $\ln(\text{weight}) = 3.147 \cdot \ln(SL) - 11.491$. There were no significant differences between slope ($F = 1.11$, $P = 0.292$) and intercept ($F = 0.006$, $P = 0.938$) for male and female regression lines.

Discussion

Our observations suggest that subtle interactions between water temperature, photoperiod, and hydrology were important proximate cues in the reproductive development and spawning readiness of the captive *L. vittata* population. A few males were ripe at 10 C; however, temperatures for maturation were ≥ 14 C, whereas females were not ripe until temperatures were ≥ 16 C. The highest frequency of reproductive maturation and spawning behavior occurred in May and June for both years. This agrees with field observations by Minckley and Carufel (1967) and C. O. Minckley (pers. comm.). The average day length during May–June in the geographic range of *L. vittata* is about 14.5 h, and stream temperatures range from 16 to 20 C (Blinn et al., 1981; Duncan and Blinn, 1989; Oberlin, 1995). This period coincides with a time of high food resources due to high productivity.

Males of the captive population were ripe at ~70 mm TL, whereas females were normally not ripe until 80 mm TL. These observations concur with field collections of *L. vittata* in Nutrioso Creek where a few ripe females < 64 mm TL had mature eggs (1.0–1.3 mm); however, most ripe females were > 75 mm TL (Blinn and Runck, unpubl). Immature females (40–50 mm) from Nutrioso Creek had gonadal weights < 0.02 g and immature eggs that ranged from 0.02–0.05 mm in diameter, whereas females with mature eggs had gonadal weights > 0.5 g with eggs ranging from 1.0–1.2 mm. The heaviest gonadal weights for male and females in Nutrioso Creek were 0.77 g (11.54 g body weight) and 2.89 g (14.39 g body weight), respectively (DWB and C. Runck, unpubl.). Average gonadosomatic indices for ripe male ($n = 15$) and female ($n = 21$) *L. vittata* in Nutrioso Creek were 4.5% (SE ± 0.5) and 11.1% (SE ± 1), respectively. Minckley and Carufel (1967) collected immature and mature eggs (0.98–1.13 mm in diameter) from females in the Little Colorado River in May with egg numbers ranging from 650 in smaller fish (50–60 mm SL) to 5600 in larger fish (approximately 100 mm SL).

Due to the importance of temperature in the reproductive development of *L. vittata*, subtle year-to-year differences in regional weather patterns and/or total degree days may greatly influence cohort survivorship and recruitment. Even a 2–3 week delay in spring warming can reduce the size of age-0 fish by as much as 14 mm TL and reduce the overwintering size of juveniles. Maximum size is important for overwintering survival because smaller age-0 fish typically store fewer winter lipid reserves than larger fish and utilize these reserves more rapidly because of relatively higher weight-specific metabolic rates (Oliver et al., 1979; Shuter et al., 1980; Thompson et al., 1991). Therefore, subtle differences in weather patterns in the Southwest may contribute to the highly variable year-to-year distribution and sporadic abundance of *L. vittata* populations throughout their geographic range.

The observed period of spawning by the captive *L. vittata* population during May and early June coincides with periods of high discharge in many southwestern streams (Fisher and Minckley, 1978; Blinn et al., 1981; Duncan and Blinn, 1989). In addition to increasing water temperatures, these periods of predictable high flows correspond with other conditions that may enhance reproductive efforts of *L. vittata* including increased water levels and hydrologic continuity, removal of fine sediments over spawning sites, increased invertebrate drift for food, increased turbidity which reduces visibility by predators, and elevated dissolved oxygen due to turbulence. It is not uncommon to find spawning of other cyprinids closely linked to spring flows and the above concomitant events (Kaeding et al., 1990; Tyus, 1991; Harvey et al., 1993). Based on observations of the captive *L. vittata* population, spawning occurred in moderate flows over gravel beds and not in standing water with fine sediments.

Minckley and Carufel (1967) suggested that a single female *L. vittata* may spawn several times per year based on observations of mature ovaries. Although we were not able to discern multiple spawns from single females, it appeared that up to three spawns occurred in the captive population each year. However, the last spawn was typically of shorter duration and yielded fewer numbers. Multiple spawnings are likely determined, in part, by the amount of food available for these opportunistic feeders (Minckley and Carufel, 1967; Runck and Blinn, 1993).

The captive *L. vittata* population provided an opportunity to study the reproductive ecology and general behavior of a threatened native fish population in the absence of other fish species. This was especially helpful due to the difficulty in taxonomically separating larvae and fry from other cyprinid species in the field. Previously, the sporadic occurrences of *L. vittata* in nature made it difficult to locate and monitor. Although conditions in the Arboretum pond were somewhat artificial, the general spawning and behavior patterns concurred with those of wild populations.

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